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Research Document 2000/006 | **Document de recherche 2000/006**

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Straying rates and stock structure of British Columbia Herring

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This document is available on the Internet at:

Ce document est disponible sur l'Internet à:

http://www.dfo-mpo.gc.ca/csas/

ISSN 1480-4883
Ottawa, 2000

Canada

102-02219/

ABSTRACT

Tag release and recovery information compiled between 1950-55 and 1980-92 for the five, major populations (stocks) of British Columbia herring were analyzed. The results indicate a high 'fidelity' rate of adult herring to the spawning area where they were tagged; 75% to 96% of tagged fish at-large for one year tended to be recovered near the spawning areas where they were released. However, these results also indicate that a significant amount of straying occurs (4-25%). A comparison between the two tagging periods indicates that the mean proportion of herring straying between populations was significantly lower in the early 1950s (7%) than it was in the 1980s (22%). The proportion of herring straying to other populations decreased exponentially with the distance between populations. Forty-one percent of the herring that strayed moved 200 km in one year, 12% moved 600 km and a few exceptional individuals (7%) dispersed a distance of 800 km. This important finding indicates that the populations are linked by an 'isolation by distance' model of gene flow. Tag recoveries during both time periods confirm that the southernmost herring populations in B.C. exchange individuals (and genes) with the most northern populations. Although there are other complicating factors, our analysis suggests that the straying rate is density-dependent -- it appears to increase linearly as the population approaches the carrying capacity of the spawn habitat. Evidence supporting this density-dependent dispersal response is apparent in 4 of the 5 major populations. Our analysis explains several stock assessment anomalies, and has significant implications for herring stock structure and management. We conclude that the high observed fidelity rate provides the biological basis for managing B.C. herring stocks, because it means that most of the adult herring that spawn in one of the major populations return to the same region to spawn the following year. Consequently, the current stock assessment areas (populations) form the basic management units. However, the significant observed straying rates also indicate that the five, major herring populations are linked by variable degrees of gene flow, and therefore form a single, large metapopulation.

RÉSUMÉ

Compilées de 1950 à 1955 et de 1980 à 1992, des données de marquage-recapture de harengs appartenant aux cinq principales populations (stocks) de la Colombie-Britannique ont été analysées. Les résultats indiquent un taux de « fidélité » élevé des harengs adultes : 75 à 96 % des poissons marqués avant qu'ils partent en haute mer pour un an ont été recapturés près des frayères où ils ont été marqués. Toutefois, des taux appréciables de vagabondage (de 4 à 25 %) ont également été observés. La comparaison entre les deux périodes de marquage montre que la proportion moyenne de

harengs qui vagabonde d'une population à une autre était significativement plus basse dans la première moitié des années 50 (7 %) que dans les années 80 (22 %). La proportion de harengs vagabonds qui se retrouvent dans une population autre que la leur décroissait exponentiellement en fonction de la distance entre les deux populations. Des harengs vagabonds, 41 % se sont déplacés de 200 km en une année, 12 % de 600 km, et quelques individus exceptionnels (7 %) ont été retrouvés à une distance de 800 km. Ce résultat important indique que le flux génique entre les populations correspond à un modèle d'« isolement par distance ». Dans les deux périodes d'étude, les recaptures confirment que les populations les plus au sud de la C.-B. échangent des individus (et donc des gènes) avec les populations les plus au nord. Malgré d'autres facteurs qui compliquent la situation, notre analyse porte à croire que le taux de vagabondage dépend de la densité : il semble croître de façon linéaire lorsque la taille de la population s'approche de la capacité de charge de la frayère. Cette dispersion dépendante de la densité est appuyée par les données caractérisant quatre des cinq principales populations. Notre analyse explique plusieurs anomalies de l'évaluation des stocks et a des répercussions importantes pour la structure et la gestion des stocks de hareng. Les auteurs concluent que le taux de fidélité élevé qu'ils ont observé offre le fondement biologique pour la gestion des stocks de hareng de la C.-B. puisque ce taux signifie que la plupart des harengs adultes qui se reproduisent dans la frayère d'une des principales populations y retournent frayer l'année suivante. Par conséquent, les zones actuelles d'évaluation des stocks (populations) constituent les unités de gestion fondamentales. Toutefois, les taux substantiels de vagabondage indiquent aussi que les cinq principales populations de hareng sont liées par des niveaux variables de flux génique, formant ainsi une seule grande métapopulation.

INTRODUCTION

A belly-tagging program designed to determine the discreteness of Pacific herring populations in B.C. began in 1936. Eighty-nine percent of the herring tagged between 1936 to 1955 were released on (or near) the spawning grounds during spring tagging operations on spawning or spent fish that were exposed to at least one fishing season (Tester 1944, Stevenson 1955, Hourston 1982). The strong tendency for these tags to be recovered in (or near) the release area, indicated that most herring return in the autumn and winter (from offshore feeding grounds) to the inshore area where they spawned the previous spring (Stevenson 1955). However, roughly one-quarter of the fish in each major population of migratory herring dispersed (strayed) to other populations (Stevenson 1955). These early studies also suggested that the amount of mixing was greatest between adjacent populations, and least between distant populations (Stevenson 1955, Taylor 1964). There was also a tendency for the numerous small, non-migratory (or resident) herring populations from inlets in the north and south Central Coast, and upper East

Coast Vancouver Island to be more isolated from neighbouring migratory and resident populations. Hourston (1959) reported that juvenile herring had a greater tendency to stray than the adults. For the West Coast of Vancouver Island population he estimated that after 2 and 3 years at liberty the 'homing' tendency was about 60% in juvenile herring compared to about 80% in adults. Consequently, it was recognised some time ago that maintenance of a population was not entirely dependent on local production, because new recruits and adults can immigrate from other herring populations (Taylor 1964).

A second tagging program was implemented in B.C. between 1979-91. In this case, herring were marked on the spawning grounds with external anchor tags (Haegele 1986). Virtually all of the tags recovered during this period came from the roe fishery, which occurred on (or very near) the spawning grounds. A preliminary analysis of the 1979-83 release data suggested that roughly 73% of the anchor tags were recovered in the stock assessment region (SAR) of release (Hay and Haegele 1987). Hay et al. (1999) have published a more recent review of the tagging data.

The purpose of this paper is to quantify the straying rates of reproductively mature herring that were at large for 1 year before capture. Specifically, for each of the five major herring populations in B.C. we examined the relationship between the distances strayed in 1 year in relation to the distances between these populations. We also determined the inter-annual variability in the straying rates for each population and one factor that appeared to modify it. Finally, we used the measured straying rates to show that the amount of biomass moving from one population to another is significant, and affects the natural mortality rate estimated by the stock assessment models.

METHODS

Major Herring Stocks

Five major, migratory herring stocks (Fig. 1) and a number of minor stocks are currently recognised in B.C. (Schweigert and Fort 1999). Accordingly, we grouped the release and recovery locations for the tags to match the boundaries of the major stocks as closely as possible, as shown in the following table:

Major Stock	Statistical Areas and Sections of Tag Release and Recovery
1. West Coast Vancouver Island (WCVI)	SA 23-25
2. Strait of Georgia (SG)	SA 14-18
3. Central Coast (CC)	SA 7 plus Sections 67 and 85
4. Queen Charlotte Islands (QCI)	Sections 21,23,24,25, and 2-6
5. Prince Rupert District (PRD)	SA 3-5

The Statistical areas shown in Fig. 1 consist of smaller spatial units called sections. For example, section 67 is in statistical area 6. The sections were originally created to group adjacent herring spawning areas into a smaller number of clusters (Haist and Rosenfeld 1988). During the anchor tag period, the location of releases and recoveries in the WCVI, CC and PRD matched the PSARC stock assessment regions exactly. The match for the SG and QCI stocks was also good, with some minor exceptions. For example, because of limitations in the precision with which tag recovery locations were recorded for QCI herring, Sections 2-5 (which are excluded from the PSARC SAR) were included in our analysis of the QCI stock.

Belly Tags. Between 1936 and 1967 metallic "Belly Tags" were applied to herring on the British Columbia coast. Most of the tagging occurred between 1936 and 1957. The tags consisted of coded metal plates that were inserted into the belly of the herring through a small incision. These tags were later recovered at the fish plants using magnetic detectors, or "induction" samplers. Tags recovered by induction provided a more precise capture location because the fish was removed from the processing line, allowing the vessel of capture to be identified. In contrast, magnetic detection occurred after the fish had been partially processed, so the vessel of capture and hence the location and specific date of capture could not be determined. Unfortunately, the majority of the belly tags were detected magnetically. Consequently, although the specific dates and locations of tag releases are known, only the season and stock assessment region of recapture were recorded consistently for the majority of tags. Like the anchor tags discussed below, we also filtered the belly tags to only select adult herring that were tagged during the spawning season and recovered 1 year later on (or near) the spawning grounds. Because the tags were recovered by the commercial fisheries, we investigated the catch database for each recovery year to ensure that the majority of the catch occurred during the spawning season. Reliable catch data are available back to the 1950/51 fishing season, so we were unable to consider tags recovered prior to the spring of 1951. During the 1950s, reduction fisheries that operated primarily between mid-November to mid-March captured the majority of herring. After the 1956/57 fishing season until the collapse of the reduction fishery in the mid-1960s, an increasing amount of the catch was taken outside this period. No tags were released in 1952. In addition, we did not include tags recovered from the 1955/56 tagging program because very few tags were recaptured, and because a straying rate could only be estimated for the Strait of Georgia stock. Accordingly, the final "Belly Tagging" database included just tags released during February to May in 1950, 51, 53 and 54, and recovered 1-year later during the 1950/51, 51/52, 53/54, and 54/55 fisheries. This amounted to 7,545 tags which were released and recovered in areas that were approximately equivalent to the five, current stock assessment regions (WCVI, SG, CC, QCI and PRD). There were commercial fisheries on all of the major stocks during

each of the recovery years, so all major stocks were sampled for possible strays. The average harvest rates during the 1951-55 recovery period (excluding 1953) averaged 60-71% of the pre-fishery biomass in the WCVI, SG CC and PRD stocks. During this period the QCI stock was harvested at a lower rate, averaging about 20%.

Anchor Tags. From 1979-91, B.C. herring were tagged with plastic intra-muscular "anchor tags". Some tags were applied during the winter or fall, however, the majority were attached during the spawning season (February to April). Most tagged herring were recovered by the commercial roe fishery, which occurred near the spawning grounds just prior to spawning. Anchor tags were recovered during the fisheries and, more frequently, at the processing plants where the roe was extracted. Anchor tagging was continuous between 1979 and 1991, with the exception of 1984 to 1987, when very few tags were released.

The purpose of our analysis was to estimate annual straying rates of reproductively mature herring, so only tags that had been released and recovered near the spawning grounds, just prior to spawning, after one year at large were included. To construct the database we filtered out any tags that were not released and recovered between February and April. During the anchor-tagging period, 572,378 tags were released. Of those, 430,193 tags were released between February and April. Of the 4,304 (1%) that were recovered, 342 had been at-large for roughly 1 year (0.9 to 1.12 years based on the known release and recovery dates). Ninety-two percent (or 315) of these tags had the recovery area known to the precision of at least the statistical area (Table 1). Five tags were released outside the five major stock assessment areas and were therefore excluded (see Table 1 footnote). The remaining 310 tags met all of our selection criteria and formed the final database (Table 1). Eight tags recovered in the Strait of Georgia in 1991 without the statistical area of recovery indicated were also included in the 310 tag database. These tags were included (under SG in Table 1) because they were all recovered in the Strait of Georgia, and excluding them may have biased straying rate estimates for this stock.

Commercial fisheries occurred in all stock areas during each of the recovery years (except in the PRD in 1983), so all of the populations were sampled for possible strays. The harvest rates in the WCVI, SG and CC populations were very similar (catch averaged 17-22% of the pre-fishery biomass). The harvest rates in the QCI and NC stocks were a little lower (9 - 11%).

The raw tagging data were not adjusted because this would require making assumptions about tag retention and survival rates, reporting rates, plant recovery efficiencies, accuracy of the estimated harvest rates, and so on. Each of these assumptions

adds more uncertainty to the data. By using the raw data, the only assumption we make is that the multifarious sources of tag loss and recovery are roughly the same in each stock assessment area.

Isolation by Distance. To determine if there was a relationship between the proportion of strays recovered in each area and the degree of separation between the release and recovery sites, we estimated the distance between the Statistical Areas or sections (for the anchor tags) and populations (for the belly tags). For the belly-tagging period, straying distances were determined by measuring the shortest path over water between the centers of each stock assessment area. This provides a rough estimate of the 'minimal' distance strayed in one year. For the anchor-tagging period, more precise straying distances were estimated by calculating the weighted mean distance strayed by each tag at the section or Statistical Area level -- using the highest precision available.

Between most of the Statistical Areas or sections there is only one possible 'minimal' straying distance. However, between locations in the Strait of Georgia and west coast of Vancouver Island, strays can migrate either through Juan de Fuca Strait (in the south) or through Johnstone Strait (in the north). In this case, we measured both distances, and choose to err on the conservative side by selecting the shortest distance as the distance strayed.

Population Size. Age-structured estimates of spawner biomass have been reconstructed for each of the five major stocks back to 1951 (Schweigert and Fort 1999). Jake Schweigert (DFO, pers. comm.) estimated the spawner biomass for 1950 using the escapement model and the available spawn data. The biomass of the Prince Rupert District stock is problematic, because the age-structured model over-estimates the biomass during both the belly and anchor tag periods (Schweigert and Fort 1999). Consequently, we were unable to evaluate the effect of population size on straying rates in the PRD stock.

RESULTS

Event Timeline. Fig. 2 illustrates the relative timing and sequence of events that transpired between tag release and recovery. After spawning, adult herring migrate to the offshore feeding grounds where age 2+ recruits, which will spawn for the first time the following spring, join them. We assume that most of the straying between populations occurs along the continental margin during the summer feeding period, when schools from adjacent populations have the opportunity to mix (e.g. Tester 1949, his Fig. 3). Some straying probably also occurs during the spring offshore migration, and the fall inshore migration to the over-wintering areas.

Fidelity and Straying Rates. To estimate interannual straying rates we restricted our analysis to the tags that were recovered after one year at-large. During the anchor tag period (1980s), 90% of the tags released between February and April were recovered in less than one year after release; 8% after one year; and only 2% after two or more years at-large. In contrast, during the reduction fishery in the early 1950s no tags released between February and April were recovered in less than one year; 62% were recovered after one year; and 38% after two or more years at-large. This difference in the recovery rate between tagging programs was primarily by design, because the anchor-tagging program was implemented to reveal *the movements of herring during the spawning season before the roe fishery*. In contrast, during the earlier belly tag period releases were designed to identify movements *after the spawning season prior to the next fishery*, which occurred from November to March, as the herring migrated from offshore feeding grounds to inshore over-wintering areas near the spawning grounds (Hourston and Haegele 1980). Occasionally, the schools failed to move inshore until they were very close to spawning (Stevenson et al 1952).

The 'fidelity rate' was defined as the proportion of tags that were recovered in the release population relative to the total number of recovered tags after one year (Hay et al. 1999). The average fidelity rates and straying rates (i.e. straying rate = 1- fidelity rate) for herring at-large for one year in each population during the early 1950s and the 1980s are summarized in Table 2. We performed an ANOVA to test for the significance of tagging period, stock, and interaction (period * stock) effects. Only the period effect was significant. During the 1950s the average fidelity rate for the WCVI, SG and CC stocks (91%) was significantly higher (ANOVA on arc sine transformed fidelity rate, $p = 0.001$) than it was during the 1980s, when it averaged 75 %.

Table 2B indicates that straying occurred without exception in every year, and in every stock, but with considerable variability between stocks and years. For example, 1951 was a low straying year for the WCVI and SG stocks, but was a high straying year for the CC and PRD stocks. In contrast, 1953 was a high straying year for the SG, but a low straying year for the WCVI and CC stocks. The average straying rate in the 1980s (21.6%) was 3 times higher than the rate (7%) in the early 1980s.

Isolation by Distance. Because the recapture sites in the 1980s were known with more precision, we used the anchor tag data to examine the relationship between the proportion of strays moving between the release and recovery areas in one year and the distance between them (Fig. 3). For the 20 possible combinations (5 populations x 4 straying possibilities), the proportion of the total number of strays migrating to other populations (Y) declined exponentially with distance (X, km): $Y = 0.75 \exp(-0.003 X)$ [$p < 0.001$]. On

average, ninety percent of the strays dispersed within 600 km of the release site. What makes these results convincing to us is that the decline in the straying rate with separation distance was apparent in every population, except the Central Coast where a relationship is not as clear (Fig. 4). Because the recapture sites were known with less precision in the 1950s, there was more scatter in the isolation by distance relationship: ($Y = 0.93 \exp(-0.003 X)$ [$p>0.05$].

The stock-specific straying patterns in both periods indicate that most of the straying occurs between adjacent populations (Table 3). In the 1980s, 79% of the strays were recovered in the two nearest populations, compared to 95% in the early 1950s. The difference between these means is highly significant (arc sine tranform t-test; $p= 0.016$), indicating a tendency for strays to disperse greater distances during the latter period. Some exceptional differences in the straying pattern are also apparent. For example, the largest proportion of strays from the Central Coast population in the 1980s moved to QCI, while relatively few strays went to the Prince Rupert District population. This pattern was reversed in the 1950s. Also, roughly equal proportions of fish strayed to the PRD and Central coasts from QCI in the 1980s, while in the 1950s most of the strays (92%) moved to the PRD, and only 6% to the Central Coast. However, we note that the harvest rate in the PRD in the 1950s was higher than it was in the other SARs so estimates of the proportion of strays recovered there could be inflated during this period.

Density-Dependent Straying Rate. To explore why the average straying rate was low in the early 1950s compared to the 1980s, we tested to see if it was related to the size of the spawning populations, which were also lower in the 1950s. To ensure that the estimates were based on a reasonable sample size, straying rates were only calculated for the years where 12 (or more) tags were recovered. This reduced the dataset to 21 population x year observations. For this comparison, population biomass was standardized by dividing the size of each spawning population in year t by the carrying capacity (K). The carrying capacity is defined as the unfished equilibrium biomass for each stock, and was obtained from Schweigert and Fort's (1999) age-structured model analysis. For the WCVI population, Ware (1996) found that the population carrying capacity varied with changes in the climate, and was much larger during the cooler period in the early 1950s. As mentioned above, the PRD was not included because the age-structured model does not produce reliable biomass and carrying capacity estimates for this population for either period (Schweigert and Fort 1999). The mean values by period for the four remaining populations are given in the following table:

Population	Period	Mean Spawner Biomass (SSB, kt)	Spawner Carrying Capacity (K, kt)	Mean SSB/K	Mean Straying Rate (%)
WCVI	1950s	14.8	66	0.22	4.9
WCVI	1980s	34.0	42	0.81	24.0
SG	1950s	36.1	86	0.42	11.9
SG	1980s	69.8	86	0.81	33.3
CC	1950s	10.7	41	0.26	9.8
CC	1980s	30.6	41	0.73	18.9
QCI	1950s	16.7	41	0.41	5.2
QCI	1980s	32.1	41	0.78	24.9

Fig. 5 shows that the straying rate increased significantly ($Y = 0.356*[SSB/K]-0.02$; adjusted $r = 0.82$, $p<0.0005$) as the biomass of spawners approached the carrying capacity. Although there is a tendency for the data to cluster around low values in the 1950s and high values in the 1980s, there is consistency in the response because the highest straying rates tended to be associated with the largest population sizes in both periods. Moreover, variations in the straying rate with population size in the 1980s are statistically significant (adjusted $r = 0.57$, $p=0.06$), indicating that the straying rate was density-dependent during this period. The data for the 1950s show the same tendency (adjusted $r = 0.43$, $p=0.09$), but are less convincing because the relationship is highly influenced by the single data point with the highest straying rate. However, we note that the straying rate increased with population size in every case (Fig. 6), which is consistent with the hypothesis that dispersal is density-dependent.

Natural Mortality Rate. The observed straying rates of herring have important implications for estimating stock productivity and natural mortality rates (M). The current value of M estimated by the age-structured model (Schweigert and Fort 1999) is actually a "net loss" rate, because it measures the net effect of three discrete processes: immigration, emigration and natural mortality.

We attempted to estimate the "probable" natural mortality rate (M_p) by accounting for the addition of new individuals by immigration, and the loss of individuals by emigration in each stock. To do this, we used several herring life history attributes and assumptions. After the fishery, the surviving adults (SB, kt) loose about 23% of their biomass during spawning (i.e. the spawn biomass (S) = 0.23*SB; Ware 1985). The

remaining adult biomass (SB - S) migrates to the offshore feeding grounds, where it is joined by the age 2+ recruits (R). These recruits will spawn for the first time the following spring. We assume that emigration (dispersal) of the adults and recruits occurs soon after the recruits have joined the adults on the offshore banks. To simplify the calculations, emigration (E) from the population and immigration (I) of new recruits and adults from other populations are assumed to occur simultaneously. The growing season for B.C. herring lasts about 8 months (approximately from March to October inclusive, (Tanasichuk 1997). Because the long-term average age-specific body weights after spawning (W_i) and the body weight a year later just prior to spawning (W_{i+1}) are known, an average growth factor for each adult age-group (i) was calculated: $GF_i = [W_{i+1} / W_i]$. The resulting age specific growth factors were then weighted by the average percentage of each age-group in the adult component of the population to yield a population growth factor (PGF). The instantaneous growth rate (G) of the adult population was obtained by taking the natural logarithm of the PGF (i.e. G = ln(PGF)). Accordingly, the natural mortality rate (M_p) was estimated from the following relationship:

$$PFB_{t+1} = B_t \exp(G - M_p). \quad (1)$$

After rearranging,

$$M_p = G - \ln (PFB_{t+1}/B_t). \quad (2)$$

Here, PFB_{t+1} is the prefishery biomass in the spring of year t+1; B_t is the biomass at the beginning of the growing season in year t (i.e. B_t = SB-S+R+I-E); and G is the instantaneous growth rate of the adult population. The estimated biomass of herring imported to, and exported from, each population annually, on average, is shown in Table 4. The results highlight several important facts: 1) each year during the 1980s, about 44 thousand tones of herring dispersed between the major stocks; 2) the WCVI and CC populations were large net importers of biomass; while 3) the Georgia Strait and QCI populations were large net exporters of biomass. We emphasise that these findings only apply to the period examined. Something appears to have affected the dynamics of the WCVI stock in 1999, because the estimated size of this stock in March 2000 was just 13,000 t prior to the fishery. So for some reason in 1999, either the export of SG herring to this area was unusually low, or the export of WCVI herring to the SG and CC stocks was unusually large, or the mortality rate was extremely high.

Time-averaged age-structured model estimates of spawner biomass, spawn, and recruit biomass for the 1980s are summarised in Table 5. This table also shows the estimated biomass exported, and imported to each population and the probable natural mortality rate (M_p). The results indicate that the WCVI stock had a high natural mortality rate (M_p = 0.69) in the 1980s, compared to the long-term average value estimated by the age-structured model (M = 0.45). In contrast, the Strait of Georgia and QCI populations had lower natural mortality rates in the 1980s (M_p = 0.30 and 0.35, respectively)

compared to the long-term average rates estimated by the age-structured model (M = 0.59 and 0.46, respectively). We obtained natural mortality estimates (M_p) similar to those in Table 5 when we assumed that only the surviving spawners disperse after spawning, and not the recruits. Consequently, the estimated value of M_p does not appear to be particularly sensitive to the assumption about age-related straying: specifically whether it is the surviving spawners, or both the recruits and surviving spawners that stray.

DISCUSSION

The tagging database has contrasting strengths and weaknesses during the two periods we examined. For the modern roe fishery period, the anchor tag data provide precise information about the recovery time and location, but suffer from a relatively low recovery rate (and hence a small sample size). In contrast, during the earlier reduction fishery period, large numbers of belly tags were recovered, but they contained less precise information about the recovery time and location. To attempt to overcome some of these weaknesses in the data, we looked for cross-period consistency in the form of the isolation by distance function, and the density-dependent straying rate relationships. With respect to the isolation by distance function, during both periods most of the straying between populations occurred within a distance of roughly 600 km; less than 10% of the strays dispersed further than this in one year. These distances are significant because they demonstrate that all five major populations are connected by dispersal. Accordingly, in only one year some herring from the most southern WCVI and SG populations can disperse to the most northern QCI and PRD populations, and vice-versa (Table 3).

Two of the three zero entries in Table 3A, which imply that no straying takes place between these populations, probably are not real. They appear to be statistical artifacts arising from the limited number of tag recoveries. Using the entire tagging database, which includes fish at large for 1 to 10 years, Hay et al. (1999) found that some herring released in PRD strayed to Georgia Strait, and that herring released in the Central Coast strayed to PRD. However, both Hay et al. (1999) and we (Tables 3A & 3B) found no evidence that herring tagged in the Strait of Georgia strayed to QCI. Accordingly, there appeared to be other factors besides distance, which can create a greater degree of isolation in some populations. In this context, we suspect that some of the small, minor herring stocks that spawn near the heads of inlets in the Central Coast region are more isolated by geography, than similar groups of herring that spawn near the coast.

Our results indicate interannual variability in straying rates (Table 2B), which is consistent with earlier findings. For example, Tester et al. (1949) examined the straying rates of herring that were belly tagged on the spawning grounds in 1948. In this case, the

tag release and recovery locations, and times were known with some precision. He found that about 6% of the herring tagged in the WCVI stock strayed to the lower SG, while about 3% of the herring tagged in the lower SG strayed to the WCVI. These results differed from the 1947 tagging returns, where immigration to the WCVI from the Strait of Georgia was greater than emigration from the WCVI to SG. Also Hay et al. (1999) found that in some years, like 1940, 1950 and 1951, for some reason more B.C. herring than usual appeared to disperse in a northerly direction. Using a more complex analytical method, Schweigert and Schwarz (1993) estimated that between 1951-54 about 3% (annually) of the PRD stock biomass had migrated there from the CC stock, and about 2% of the CC biomass came from the PRD. For comparison, our calculations (Table 4) suggest that during the 1980s about 5.6% of the CC stock came from the PRD (i.e. 1.6 kt / [28.5-5.5+5.4]kt), while very little of the PRD biomass came from the CC stock.

Tester et al. (1949) found that straying also occurs between the major, southern West Coast of Vancouver Island herring population (SA 23-25) and the minor, northern population (SA 26 & 27). More recent data summarized by Hay and Haegele (1987) suggest that 24% of the herring in the SW coast of Vancouver Island migrated to NW Vancouver Island between 1937-64. For the 1946-50 period Schwarz et al. (1993) also reported a movement of herring from the SW coast of Vancouver Island to NW Vancouver Island. These observations suggest a 'stepping stone' model of dispersion: with some fish moving from the SWCVI to NWCVI to Central Coast to QCI and PRD (and vice versa). We suspect that significant mixing, and subsequent straying, of the SG and WCVI stocks occurs on the summer feeding grounds on the continental margin in areas 121, 123 and 124 (Fig. 1). And also between the WCVI, SG and CC stocks around the Goose Islands and Cook Banks (SA 108-111; Fig. 1). Support for this hypothesis comes from Taylor (1973), who noted that tag "recoveries in the summer of 1964 indicate that some herring from the lower central population feed in the summer off the northern tip of Vancouver Island...".

Hay et al.(1999) estimated the fidelity rate for the five major herring populations for the entire tagging database (1936-91). The average fidelity rates ranged from 82% to 95%, which corresponds to average straying rates of 18% to 5%. This range in estimates is similar to the range we obtained for the 1950-54 and 1980-91 periods. However, we found a significant difference between the average fidelity (and straying) rates in these two periods, which appeared to be linked to variations in stock density (Fig. 5).

From an evolutionary perspective, we believe there is a selective advantage for the dispersal rate of herring to increase with the relative size of the spawning stock (i.e. SSB/K). Pacific herring is an iteroparious species. But the B.C. stocks have a relatively high natural mortality rate (average $M=0.46\ yr^{-1}$). Hence, the reproductive lifespan of

most herring is only a few years. When the size of the spawning stock approaches its carrying capacity (K), density-dependent stock-recruitment dynamics dictate that the resulting recruits/spawner will be low. Accordingly, as the suitability of the spawn habitat decreases it may be advantageous in the long run for some surviving spawners to disperse to other areas to reproduce. Presumably, some of the individuals that migrate to other populations will produce more recruits/spawner over their short reproductive lifespan if the density of spawners in the destination stock is lower, relative to its carrying capacity, than it was in the source stock.

The results summarised in Table 5 suggest that during the 1980s the WCVI population appeared to have a higher natural mortality rate ($M_p = 0.69$) than the other major herring populations. This finding is consistent with the observation that water temperatures were above normal in the 1980s, and that more Pacific hake migrate to the WCVI in warm summers to forage (Ware and McFarlane 1995). Hake is a significant herring predator along the West Coast of Vancouver Island in the summer (Tanasichuk et al. 1991; Ware and McFarlane 1995). Hence, the WCVI population probably experienced higher predation rates during the 1980s than the other major herring populations, which are normally exposed to a smaller biomass of resident predators. The low natural mortality rate of Georgia Strait herring in the 1980s is an interesting anomaly. Perhaps, differences in the summer distribution patterns of these two stocks during this period resulted in WCVI herring being more vulnerable to hake predation.

The fact that herring disperse to other populations is important because: 1) it prevents the loss of genetic heterozygosity within populations due to genetic drift; 2) it results in the colonization of vacant or new spawning habitat; and 3) it significantly increases the persistence time of the population. Genetic research has established that inbreeding depression in small isolated populations typically leads to adaptive decline and extinction. A small amount of gene flow between partially isolated populations is necessary for long term persistence. Mills and Allendorf (1996) suggested that 1 to 10 immigrants per generation will minimize the loss of polymorphism and heterozygosity within populations due to genetic drift, while allowing for divergence in allele frequencies among populations. The straying rates that we observed are far in excess of the 1 to 10 immigrants per generation required to oppose population divergence by genetic drift. Assuming that the immigrants are just as likely to survive and breed as the residents, the high straying rates of B.C. herring will tend to reduce the genetic divergence among the five, major populations. However, some limited divergence may occur, because these populations live and spawn in different environments, and therefore probably experience somewhat different natural selection pressures.

McQuinn (1997) in a recent review, concluded that herring stock structure and dynamics are consistent with a metapopulation concept, which holds that the population structure of many species consists of an array of populations linked by variable degrees of gene flow. In metapopulation theory, migrants establish new local populations that persist for some time and, in turn, send out their own migrants, which colonize new areas and mix with other local populations. Since some local populations can disappear due to natural causes, migrants are necessary for the survival, expansion and persistence of the metapopulation. If suitable habitat varies over space and time, the persistence time of a population increases significantly when there is movement between populations (Roff 1974). The extensive evidence for straying in Pacific herring demonstrates that the five major B.C. populations form a large metapopulation. In this context, the high observed fidelity rate provides the biological basis for managing B.C. herring stocks, because it ensures that most of the individuals that spawn in one of the major populations return to the same area to reproduce the following year. Consequently, the current five stock assessment regions form the appropriate management units. However to improve the forecasting accuracy of the stock assessment models, the demographic and management implications of straying by B.C. herring need to be evaluated, and included in future stock assessment models.

CONCLUSIONS

There are several lines of evidence in the tagging and spawn databases, which support the hypothesis that the five large, migratory herring populations in B.C. form a spatially structured metapopulation:

1. The spawning habitat can be characterised as a patchy, fragmented landscape (Hourston 1980). At the section level of spatial aggregation, there is recurring evidence in the spawn records of disappearance and recolonization events (Hay et al 1991). These events are expected to occur in metapopulations.

2. The tagging data indicate significant straying between the five, major B.C. herring populations. The straying pattern matches an *isolation by distance* model. Accordingly, there may be some limited genetic divergence between distant major stocks, and some geographically isolated, minor stocks.

3. The straying rate tends to increase with the size of the spawning stock. Accordingly, straying rates were higher in the 1980s, when the stocks were closer to their carrying capacities, than they were in the 1950s, when the stocks were reduced by high harvest rates.

4. During the 1980s, about 44 thousand tonnes of herring dispersed each year between the major stocks. The WCVI and Central Coast stocks were *net importers* of adult biomass; the Georgia Strait and QCI stocks were *net exporters*; while the PRD stock was roughly neutral.

5. Current stock assessment model estimates of natural mortality (M) are confounded by dispersal. When dispersal is considered, the WCVI and Central Coast stocks have higher M's, and the Georgia Strait and QCI stocks lower M's than age-structured model estimates. The very high M for the WCVI stock is consistent with field studies, which found that the WCVI stock was exposed to high hake predation in the 1980s.

6. The high fidelity rate at the population level provides the biological basis for managing B.C. herring stocks, because it means that most of the adult herring that spawn in one of the major populations return to the same region to reproduce the following year. Consequently, the current stock assessment areas (populations) form the appropriate management units.

7. Density-dependent dispersal, and other dispersal-modifying factors, reduce the accuracy of stock assessment model forecasts of recruitment and returning adult biomass. Consequently, the demographic and management implications of straying by B.C. herring need to be evaluated and, if necessary, included in future stock assessment models.

ACKNOWLEDGEMENTS

This was a collaborative project between the Department of Fisheries and Oceans and the Herring Conservation and Research Society. We are grateful to the Herring Conservation and Research Society for providing the funding for Christine Tovey to participate in this study. We also thank K. Daniel for her advice in using the tagging database, and Jake Schweigert for estimates of spawner biomass.

REFERENCES

Haegele, C.W. 1986. Returns from anchor taggings of herring in British Columbia, 1979 to 1985. Can. Data Rept. Fish. Aquat. Sci. 582. 129 p.

Haist, V. and L. Rosenfeld. 1988. Definitions and codings of localities, sections, and assessment regions for British Columbia herring data. Can. MS Rep. Fish. Aquat. Sci. 1994: 123 p.

Hay, D.E., P.B. McCarter, R. Krinlund and C.Roy. 1989. Spawning areas of British Columbia herring. A review, geographical analysis and classification. Volume VI: West Coast Vancouver Island. Can. Rep. Fish. Aquat. Sci. 2019:213 p.

Hay, D.E. and C.W. Haegele. 1987. A review and overview of the geographical distribution and migrations of herring stocks in B.C. with implications for management. PSARC working paper H87-5:17 p.

Hay, D.E., P.B. McCarter and K. Daniel. 1999. Pacific herring tagging from 1936-1992: A re-evaluation of homing based on additional data. Can. Stock Ass. Sec. Res. Doc. 99/176: 58 p.

Hourston, A.S.1959. The relationship of the juvenile herring stocks in Barkley Sound to the major adult herring population in British Columbia. J. Fish. Res. Bd. Can. 16:309-320.

Hourston, A.S.1982. Homing by Canada's west coast herring to management units and divisions as indicated by tag recoveries. Can. J. Fish. Aquat. Sci. 39:1414-1422.

Hourston, A.S. and C.W. Haegele. 1980. Herring on Canada's Pacific coast. Can. Spec. Publ. Fish. Aquat. Sci. 48:23 p.

McQuinn, I.H. 1997. Metapopulations and the Atlantic herring. Rev. Fish Biol. and Fisheries 7:297-329.

Mills, L.S. and F.W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology, 10: 1509-1518.

Roff, D.A. 1974. Spatial heterogeneity and the persistence of populations. Oecologia 15: 245-258.

Schwarz, C.J., J.F. Schweigert and A.N. Arnason. 1993. Estimating migration rates using tag-recovery data. Biometrics 49:177-193.

Schweigert, J.F. and C.J. Schwarz. 1993. Estimating migration rates for Pacific herring *(Clupea pallasi)* using tag-recovery data. Can. J. Fish. Aquat. Sci. 50:1530-1540.

Schweigert, J. and C. Fort. 1999. Stock assessments for British Columbia herring in 1999 and forecasts of the potential catch in 2000. Can. Stock Ass. Sec.Res. Doc. 99/178: 96 pp.

Stevenson, J.C. 1955. The movement of herring in British Columbia waters as determined by tagging with a description of tagging and tag recovery methods. Cons. Int. Explor. Mer. Rapp. et Proc.-Verb. 140:33-34

Stevenson, M.A., A.S. Hourston, and J.A. Lanigan. 1952. Results of the west coast of Vancouver Island herring investigation, 1950-51. Rept. British Columbia Fish. Dept. 1952, pp. 51-84

Tanasichuk, R.W. 1997. Influence of biomass and ocean climate on the growth of Pacific herring *(Clupea pallasi)* from the southwest coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 54:2782-2788.

Tanasichuk, R.W., D.M. Ware, W. Shaw and G.A. McFarlane. 1991. Variations in the diet, daily ration, and feeding periodicity of Pacific hake *(Merluccius productus)* and spiny dogfish *(Squalus acanthias)* off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 48: 2118-2128.

Taylor, F.H.C. 1964. Life history and present status of British Columbia herring stocks. Bull. Fish. Res. Board. Can. 143: 81p.

Taylor, F.H.C. 1973. Herring tagging experiments, 1957-67. Fish. Res. Bd. Can. Tech. Rep. 422: 31 p.

Tester, A. 1944. Tag returns from Kwakshua Passage herring, 1943-44. Fish. Res. Bd. Can. Pacific Biological Station Progress Report 59: 3-6.

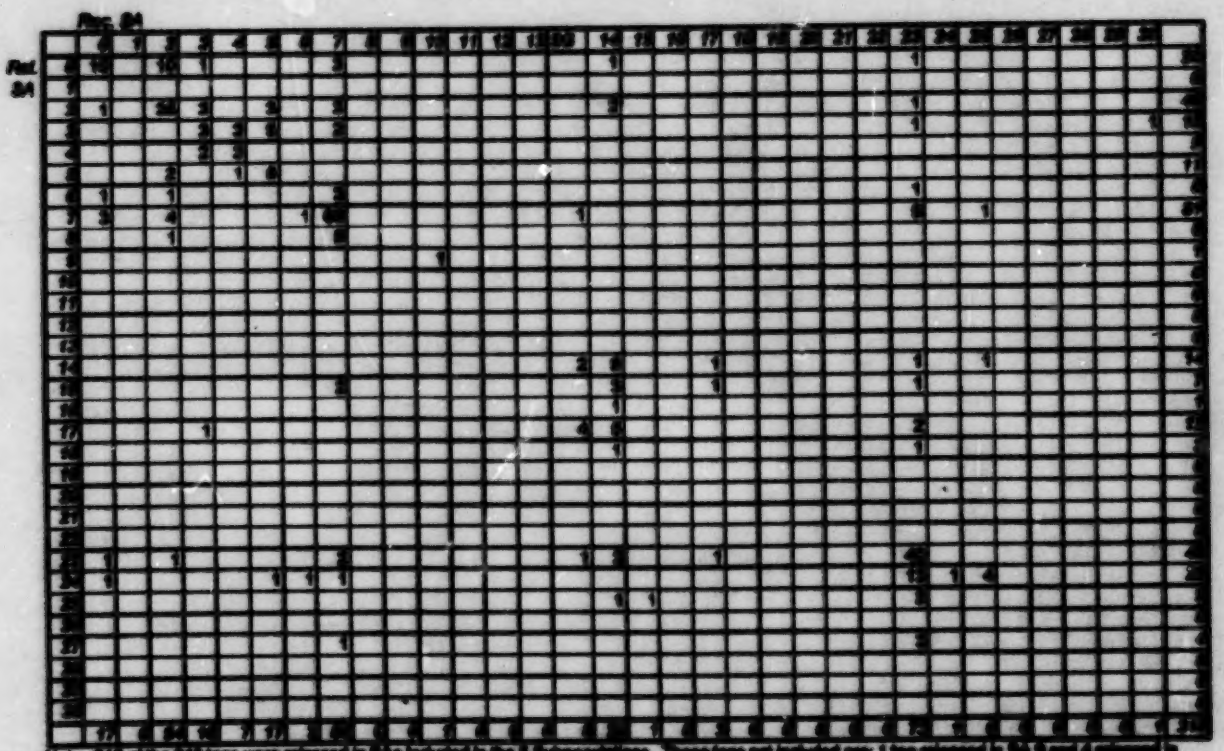
Tester, A.L. and J.C. Stevenson. 1949. Results of the west coast of Vancouver Island herring investigation, 1947-48. Rept. British Columbia Fish. Dept. 1949, pp. 41-86

Ware, D.M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring *(Clupea harengus pallasi)*. Can. J. Fish. Aquat. Sci. 42:127-137.

Ware, D.M. 1996. Herring carrying capacity and sustainable harvest rates in different climate regimes. Pac. Stock Assess. Rev. Comm. Working Paper H96-3. 19p.

Ware, D.M. and G.A. McFarlane. 1995. Climate induced changes in Pacific hake *(Merluccius productus)* abundance and pelagic community interactions in the Vancouver Island upwelling system. p. 509-521. In R.J. Beamish [ed.] Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121.

Table 1. Number of herring tags released in each statistical area (SA) between Feb.-April 1990-1991 that were recovered the following Feb.-April (1991-1992) in each statistical area. Only herring at-large for 1 complete year are included in this table.



Note: 510 of the 515 tags were released in SAs included in the 8 Subpopulations. These tags not included are: 1 tag released in SA 9 and 4 released in SA 37. 8 tags recovered in the Straight of Georgia in 1991 that did not have the recovery SA 'known' were added to the table in the "Oth" column.

Table 2A. Interannual variability in the stock assessment region fidelity rates for years with 12 or more tag returns. The fidelity rate was calculated as x/y, where x is the number of tags at large for one year that were recovered in the area of release in the release year + 1, and y is the total number of tags at large for one year that were recovered in the release year +1. Note that some tags were recovered in 1954 and 1980-83 in all stock areas. In 1988 tags were only recovered in PRD. However, in all cases less than 12 tags were recovered, so the results are not shown because of the small sample size.

Release Year	WCVI (SA 23,24,25)	Georgia Strait (SA 14-18)	Central Coast (SA 6,7,8,9)	QCI (SA 0,2)	PRD (SA 3,4,5)
1950	0.888	0.833	0.902	.	0.958
1951	0.992	0.972	0.856	.	0.942
1953	0.974	0.739	0.960	.	0.983
1954	.	0.976	0.889	0.948	0.968
1981	.	.	.	.	.
1982	0.850	.	.	.	.
1988	.	.	.	.	.
1989	0.687	0.667	0.806	.	.
1990	0.739	0.667	0.816	0.644	.
1991	.	.	.	0.857	.
Average	0.855	0.809	0.871	0.816	0.963

Table 2B. Interannual variability in straying rates from each population, in years where 12 or more tags were recovered. The straying rate was calculated as (1- x/y), where x is the number of tags at large for one year that were recovered in the indicated stock area in the release year + 1, and y is the total number of tags at large for one year that were recovered in the release year +1. Hence the straying rate = (1- fidelity rate). Note that there were no releases or recoveries in SA19, 28 and 29 or in Section 132, so the straying rates estimated for the Georgia Strait do not include herring from these areas.

Release Year	WCVI (SA 23,24,25)	Georgia Strait (SA 14-18)	Central Coast (SA 6,7,8,9)	QCI (SA 0,2)	PRD (SA 3,4,5)
1950	0.112	0.167	0.098	.	0.042
1951	0.008	0.028	0.144	.	0.058
1953	0.026	0.261	0.040	.	0.017
1954	.	0.024	0.111	0.052	0.032
1981	.	.	.	.	.
1982	0.150	.	.	.	.
1988	.	.	.	.	.
1989	0.313	0.333	0.194	.	.
1990	0.261	0.333	0.184	0.356	.
1991	.	.	.	0.143	.
Average	0.145	0.191	0.129	0.184	0.037

Table 3A. Straying pattern. Percent of strays from the releases in each population (between 1980-91) recovered in other populations one year later (in the next spawning season). The populations where the fish were tagged and released are listed in the rows in the table, and the recovery areas in the columns. For example, 15 tags recovered from the WCVI population strayed to other populations; 46.7 of these tags were recovered in Georgia Strait, 26.7 % were recovered in the Central Coast, and so on. Accordingly, the percentages across each row sum to 100%.

	WCVI	SG	CC	QCI	PRD	SEA	# Strays
1. WCVI	•	46.7	26.7	20.0	6.7	0	15
2. SG	66.7	•	22.2	0	11.1	0	9
3. CC	38.9	5.6	•	55.6	0	0	18
4. QCI	11.1	16.7	33.3	•	38.9	0	18
5. PRD	16.7	0	33.3	33.3	•	16.7	6

Notes: SEA means south-east Alaska.

Table 3B. Straying pattern. Percent of strays from the releases in each population (between 1950-54) recovered in other populations one year later during the next spawning season. The population where the fish were tagged and released are listed in the rows, and the recovery areas in the columns. For example, 95 tags recovered from the WCVI population strayed to other populations; 53.7 of these tags were recovered in Georgia Strait, 45.3 % were recovered in the Central Coast, and so on. Accordingly, the percentages across each row sum to100%.

	WCVI	SG	CC	QCI	PRD	# Strays
1. WCVI	•	53.7	45.3	0	1.0	95
2. SG	86.5	•	9.6	0	3.8	52
3. CC	4.3	3.4	•	0	92.3	351
4. QCI	2.9	0	5.6	•	91.7	36
5. PRD	4.5	4.5	75.0	15.9	•	44
6. Wash.	50.0	50.0	0	0	0	2

Notes: Wash. means Washington State.

Table 4A. Net Import of biomass *to* the WCVI stock (SP1) from the other major herring populations in the 1980s. P (x,1) indicates the proportion of strays from the source population SP(x) that disperse to SP(1).

Source SP (x)	Source SP (kt in year t)[1]	Straying rate	P(x,1)	Import (kt)
SG (SP2)	65.2	0.250	0.667	10.9
CC (SP3)	28.5	0.194	0.389	2.1
QCI (SP4)	48.5	0.243	0.111	1.3
PRD (SP5)	24.1	0.194	0.167	0.8
			Total Imported to WCVI	15.1
	WCVI Biomass = 34.2 kt	WCVI Export rate = 0.197	Total Exported from WCVI	6.7
			Net Import to WCVI	**+ 8.4**

1. Source SP(kt) = SB (yr t) - Spawn (yr t) + Recruit Biomass (yr t+1). Where spawn = 0.23*SB

Table 4B. Net Import of biomass *to* the Georgia Strait stock (SP2) from the other major herring populations in the 1980s. P(x,2) indicates the proportion of strays from the source population SP(x) that disperse to SP(2).

Source SP (x)	Source SP (kt in year t)[1]	Straying rate	P(x,2)	Import (kt)
WCVI (SP1)	34.2	0.197	0.467	3.1
CC (SP3)	28.5	0.194	0.056	0.3
QCI (SP4)	48.5	0.243	0.167	2.0
PRD (SP5)	24.1	0.194	0.000	0.0
			Total Imported to SG	5.4
	SG Biomass = 65.2 kt	SG Export rate = 0.250	Total Exported from SG	16.3
			Net Import to SG	**- 10.9**

1. Source SP(kt) = SB (yr t) - Spawn (yr t) + Recruit Biomass (yr t+1). Where spawn = 0.23*SB

Table 4C. Net Import of biomass *to* the Central Coast stock (SP3) from the other major herring populations in the 1980s. P (x,3) indicates the proportion of strays from the source population SP(x) that disperse to SP(3).

Source SP (x)	Source SP (kt in year t)[1]	Straying rate	P(x,3)	Import (kt)
WCVI (SP1)	34.2	0.197	0.267	1.8
SG (SP2)	65.2	0.250	0.222	3.6
QCI (SP4)	48.5	0.243	0.333	3.9
PRD (SP5)	24.1	0.194	0.333	1.6
			Total Imported to CC	10.9
	CC Biomass = 28.5 kt	CC Export rate = 0.194	Total Exported from CC	5.5
			Net Import to CC	+ 5.4

1. Source SP(kt) = SB (yr t) - Spawn (yr t) + Recruit Biomass (yr t+1). Where spawn = 0.23*SB

Table 4D. Net Import of biomass *to* the QCI stock (SP4) from the other major herring populations in the 1980s. P (x,4) indicates the proportion of strays from the source population SP(x) that disperse to SP(4).

Source SP (x)	Source SP (kt in year t)[1]	Straying rate	P(x,4)	Import (kt)
WCVI (SP1)	34.2	0.197	0.200	1.3
SG (SP2)	65.2	0.250	0.000	0.0
CC (SP3)	28.5	0.194	0.556	3.1
PRD (SP5)	24.1	0.194	0.333	1.6
			Total Imported to QCI	6.0
	QCI Biomass = 48.5 kt	QCI Export rate = 0.243	Total Exported from QCI	11.8
			Net Import to QCI	- 5.8

1. Source SP(kt) = SB (yr t) - Spawn (yr t) + Recruit Biomass (yr t+1). Where spawn = 0.23*S

Table 4E. Net Import of biomass *to* the Prince Rupert District stock (SP5) from the other major herring populations in the 1980s. P (x, 5) indicates the proportion of strays from the source population SP(x) that disperse to SP(5).

Source SP (x)	Source SP (kt in year t)[1]	Straying rate	P(x,5)	Import (kt)
WCVI (SP1)	34.2	0.197	0.067	0.4
SG (SP2)	65.2	0.250	0.111	1.8
CC (SP3)	28.5	0.194	0.000	0.0
QCI (SP4)	48.5	0.243	0.389	4.6
			Total Imported to PRD	6.8
	PRD Biomass = 27.6 kt	PRD Export rate = 0.194	Total Exported from PRD	4.7
			Net Import to PRD	+ 2.1

1. Source SP(kt) = SB (yr t) - Spawn (yr t) + Recruit Biomass (yr t+1). Where spawn = 0.23*SB

Table 5. Estimated natural mortality rate (M_p) calculated from age-structured model estimates of spawner biomass (Schweigert and Fort 1999), the long-term average instantaneous growth rate (G), and the estimated export and import of biomass to each population during the anchor tagging period (1980-91). The calculated value of M_p considers the growth and mortality of the surviving spawners *and* the new recruits, which are presumed to join the adults at the beginning of the growing season on the offshore banks. The calculations assume that the recruits mix with the surviving spawners, and therefore stray at the same rates. For comparison, M is the natural mortality rate estimated by the age-structured model, which implicitly assumes there is no movement of biomass between populations (Schweigert and Fort 1999).

Population	Spawner Biomass (SB, kt)	Spawn (kt)	Recruits (kt)	Import (kt)	Export (kt)	B_0 (kt)	B_{210} (kt)	G	M_p	M
1. WCVI	29.9	6.8	11.1	**15.1**	6.7	42.6	33.1	0.44	0.69	0.45
2. SG	53.3	12.1	24.0	5.4	**16.3**	54.3	62.5	0.44	0.30	0.59
3. CC	26.9	6.1	7.7	**10.9**	5.5	33.9	33.0	0.43	0.46	0.28
4. QCI	41.9	9.5	16.1	6.0	**11.8**	42.7	45.4	0.41	0.35	0.46
5. PRD	15.2	3.4	12.4	6.8	4.7	26.2	23.7	0.42	0.52	0.52
Sum (or average)	167.2	38.0	71.3	44.2	45.0	199.7	197.7	0.43	0.46	0.46

Note: 1. The slight difference between the total export and import of adult biomass is due to the export of about 800 t of fish to SE Alaska from the PRD. 2. The probable M was estimated from the following equation: $M_p = G - \ln (B_{210} / B_0)$; where
$B_0 = [SB - Spawn + Recruits] - Export + Import$; $B_{210} = PFB_{(t+1)}$; and $Spawn = 0.23 * SB$

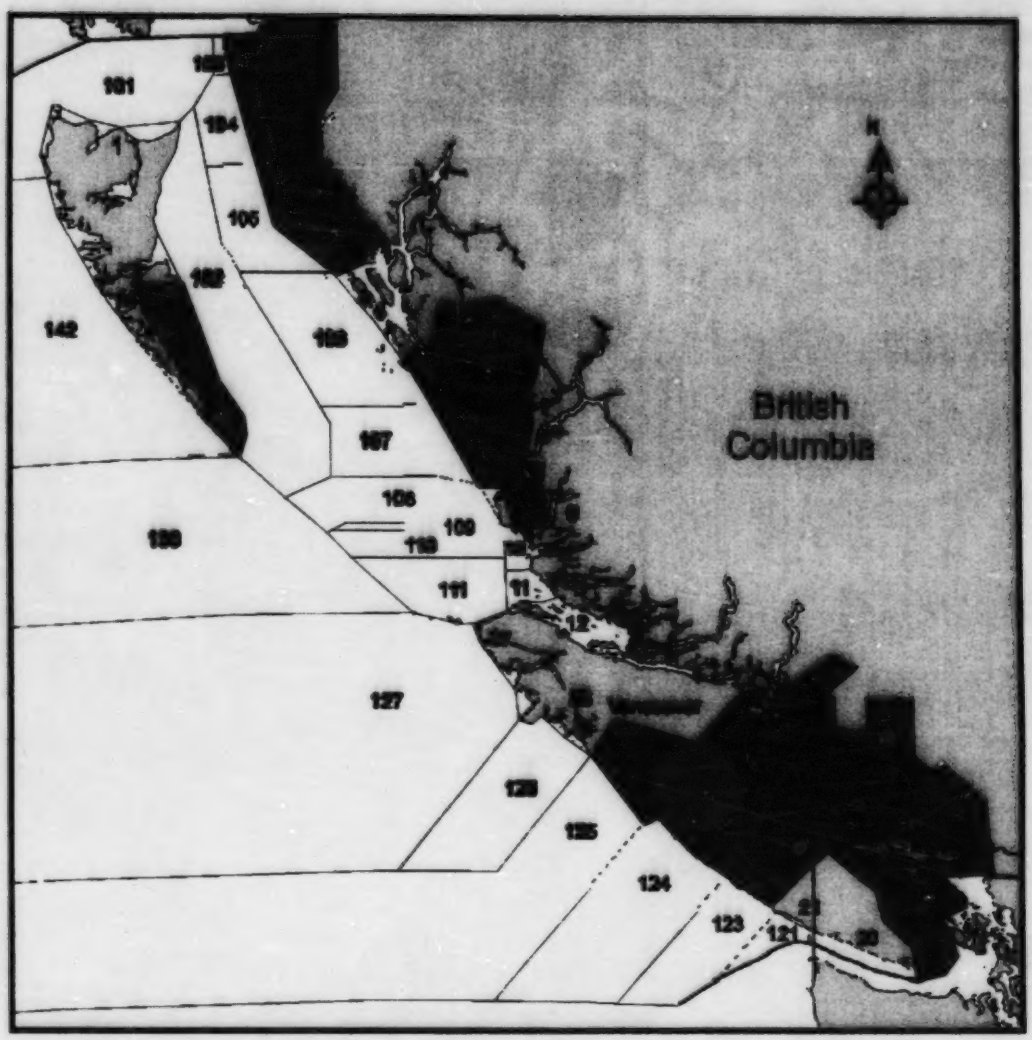


Figure 1. Current five stock assessment regions (dark grey shading), which delineate the major, migratory herring populations, in British Columbia. The numbers indicate the Statistical Areas mentioned in the text.

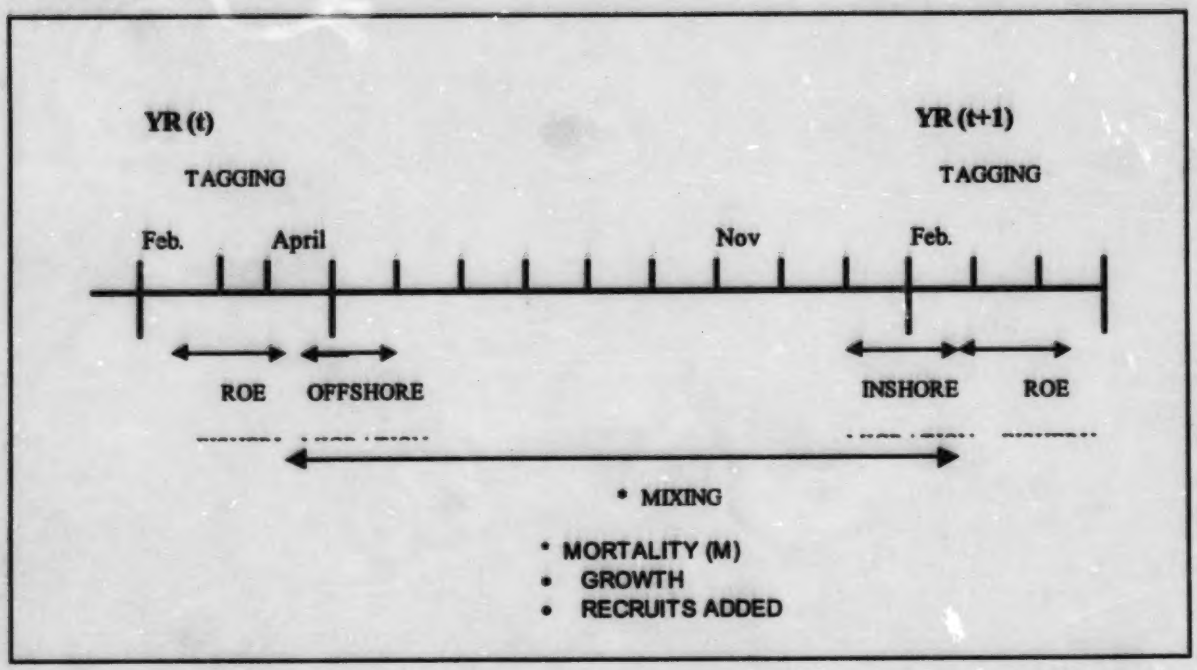


Figure 2. Time/event line for the tagging, offshore migration, and recapture of herring between 1980 and 1992. Only tags released and recovered during the spawning season (February to April) were used for the straying analysis. Tagged herring were recovered in the roe fishery, which occurred primarily in March, near the spawning grounds. Most of the mixing, and subsequent straying of herring from one population to another, occurs on the offshore feeding grounds.

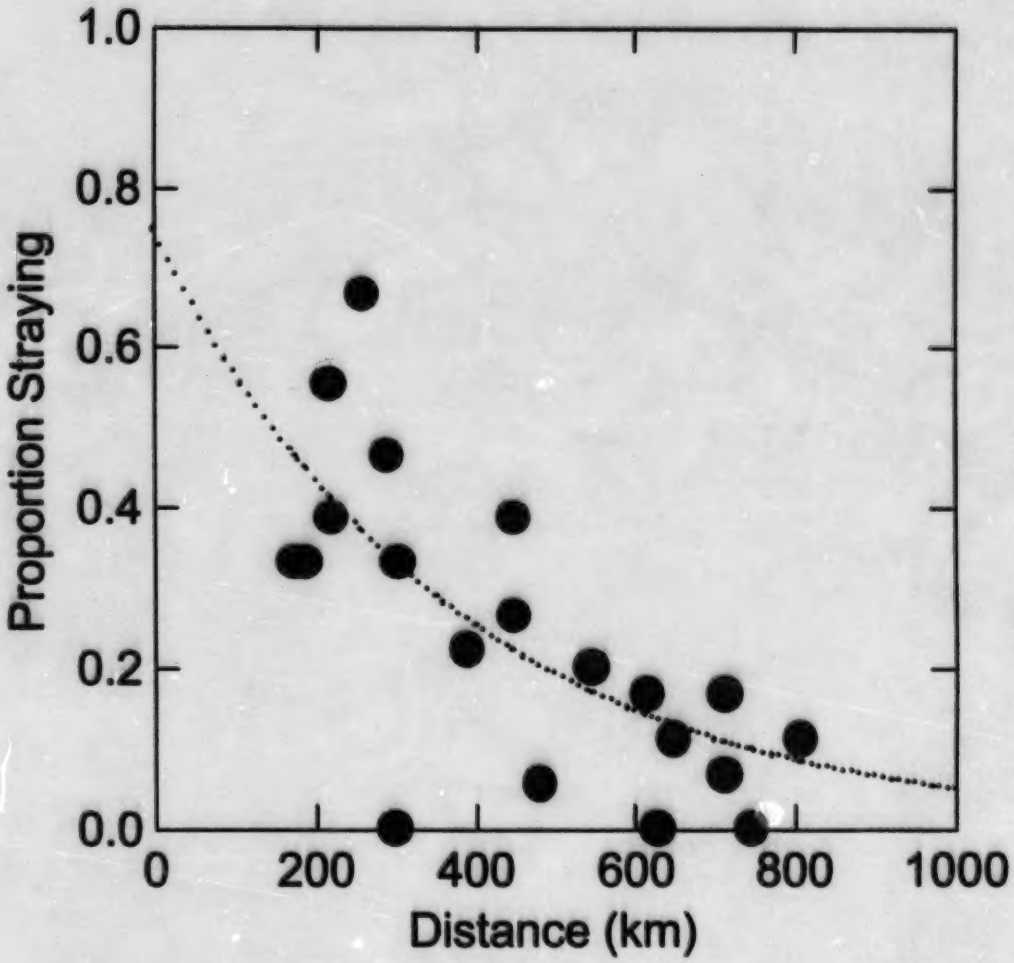


Figure 3. Isolation by distance relationship for B.C. herring . The points indicate the proportion of herring straying to other populations, as a function of the distance between the populations. For example, the data indicate that roughly 41% of the herring that strayed were recovered a year later in another population, which was about 200 km away. The twenty data points indicate the results for each of the 5 x 4 possible straying combinations. The fitted negative exponential function (curve) is highly significant.

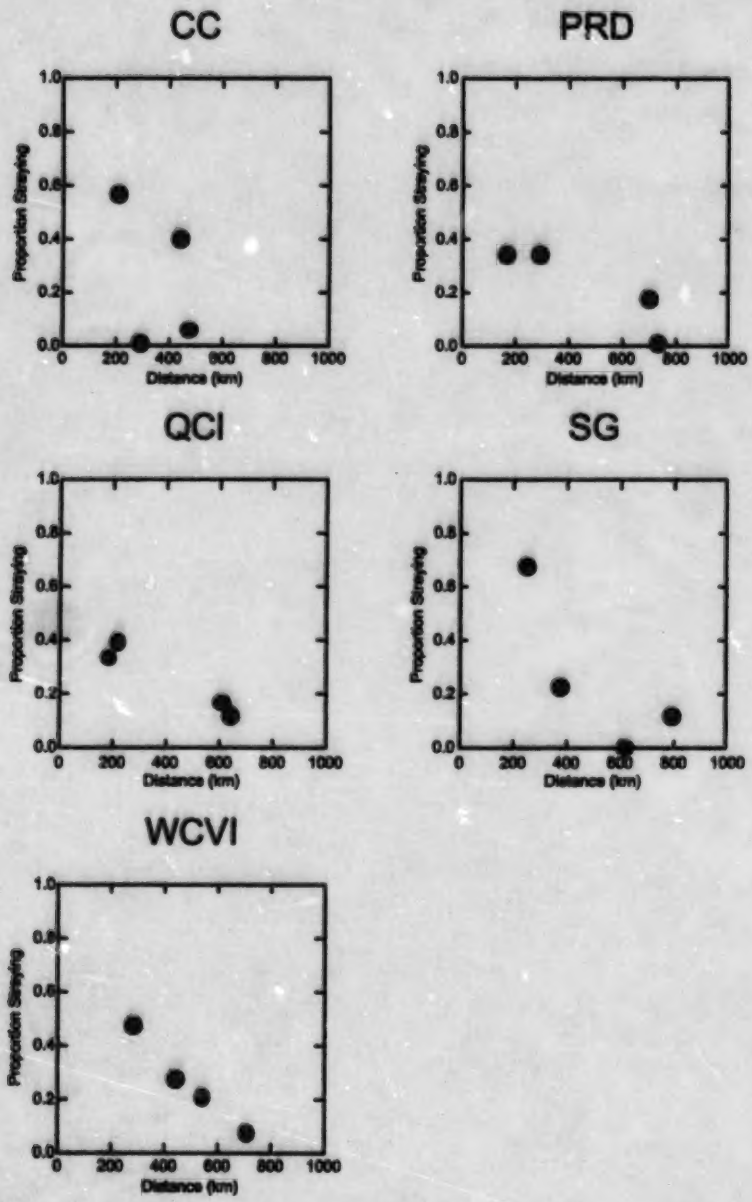


Figure 4. Isolation by distance relationship for each populaton during the 1980s. A decline in the straying frequency with distance is apparent in all but the Central Coast (CC) stock.

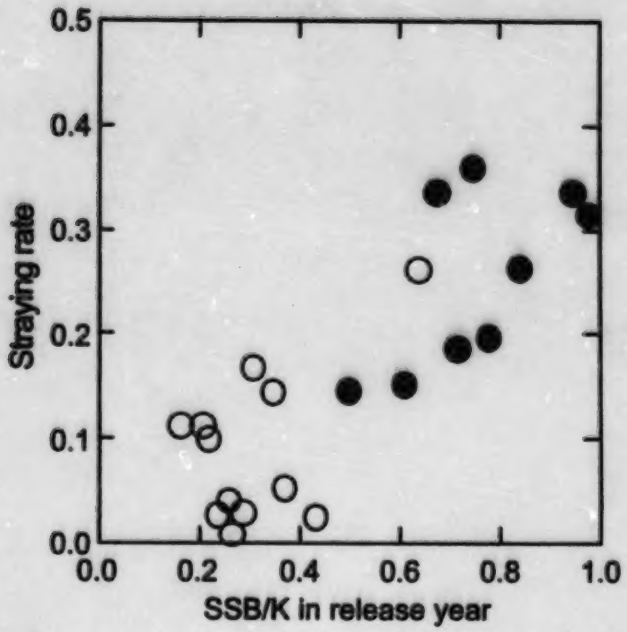


Figure 5. Density-dependent change in the straying rate. The x-axis indicates the spawning biomass of each population (except PRD, see text) relative to its carrying capacity (K) in the release year. The solid circles indicate the straying rates during the 1980s, and the open circles the straying rates during the 1950s.

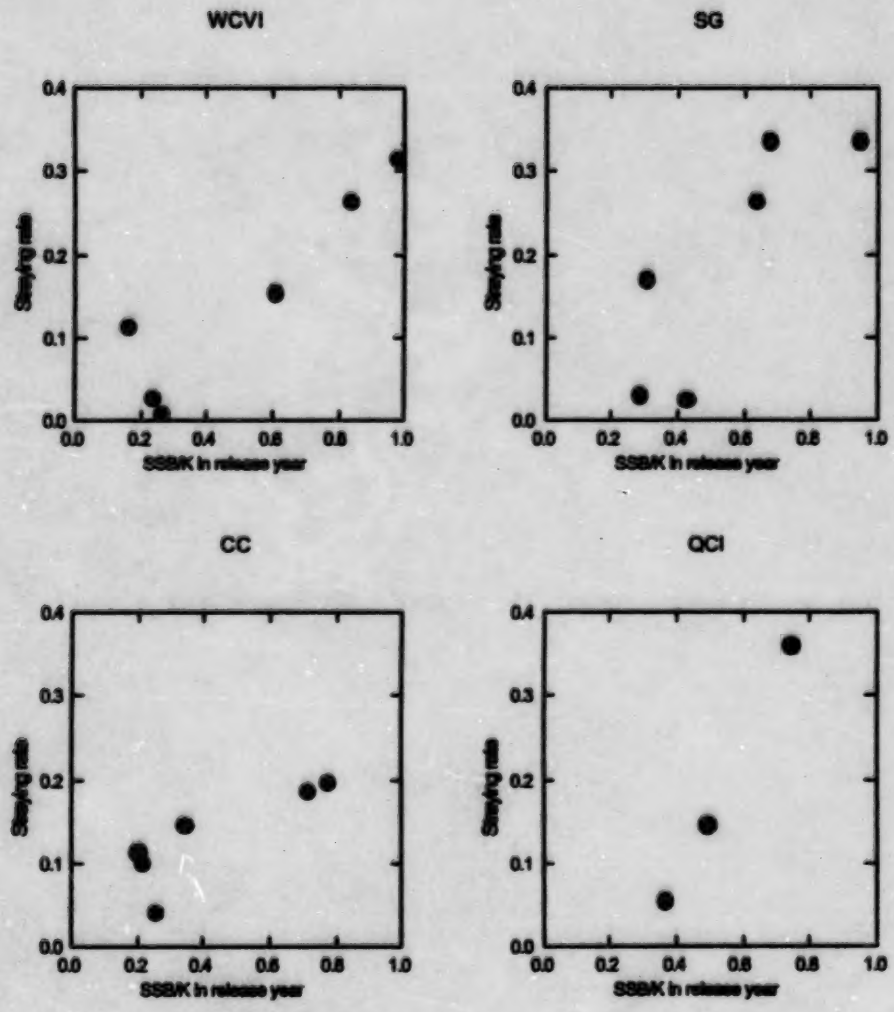


Figure 6. Density-dependent relationship between the straying rate and SSB/K in the release year in the West Coast of Vancouver Island, Strait of Georgia, Central Coast, and Queen Charlotte Islands populations.